

Native Hawaiian Cotton (*Gossypium tomentosum* Nutt.)¹

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ALTHOUGH THE WILD COTTON, *Gossypium tomentosum* Nutt., is one of the more common of the few endemic species which still survive on the coastal plains of the Hawaiian Islands, it remains relatively unknown to the geneticist. Elsewhere it has been grown with indifferent success in experimental culture. Under such diverse conditions as those found in the West Indies, southern Mexico, the U. S. cotton belt, and in greenhouse culture, it flowers sparingly and even less frequently sets seeds. As a consequence, experimental studies have been very restricted, and cytogenetic analysis has been confined almost entirely to the few crosses which have been made with annual forms of the related New World species, *G. barbadense* L. and *G. hirsutum* L. To the technical difficulties may be added the lack of representative collections of the species in culture. The few accessions studied have usually been obtained from the more readily available Oahu populations, and less frequently from Molokai. These have been supplied to cotton geneticists through the courtesy of resident Hawaiian botanists, J. F. Rock, O. Degener, A. Mangelsdorf, and others, and patiently resupplied as fast as the stocks in culture expired.

As seen in culture, the different accessions show little morphological variation (finely tomentose vegetative parts, sulphur-yellow and spotless flowers, long anther filaments partly fused in pairs, nectariless leaves, and undifferentiated seed fibers). More recently, visitors to the islands, unacquainted with the taxonomy of the species, have sent seed samples to the mainland, and the plants grown from some of these appear to differ rather widely from earlier "authentic" accessions.

It has long been recognized that an understanding of the degree of relationship existing between *G. tomentosum* and the other 52-

chromosome species of *Gossypium* is fundamental for a satisfactory interpretation of the evolution of the genus as a whole. It is somewhat disturbing for the cytogeneticists not to know if the limited samples of the species studied in culture are at all representative of its natural range of variation, nor to be confident that some of the "off-types" which have been collected recently may safely be attributed to the effects of hybridization with those 19th-20th century introductions of *barbadense* and *hirsutum* which still persist in the islands (Stephens, 1963).

In the spring semester, 1963, a temporary appointment to the staff of the Genetics Department, University of Hawaii, gave me the opportunity to make a field study of the native species. I should like here to record my thanks to the University of Hawaii for inviting me to their campus and to my home institution, North Carolina State College, for granting me the necessary leave of absence. Thanks are also due to the National Science Foundation for defraying a major part of the travel expenses (NSF Grant G-14203).

GEOGRAPHICAL RANGE

G. tomentosum has never been found beyond the limits of the Hawaiian Islands. Statements to the contrary have arisen through nomenclatural confusion (Watt, 1907:69-71).³ Hillebrand's statement (1888:51) that it occurred on all the Hawaiian Islands probably referred only to some or all of the eight major islands of the group—Niihau, Kauai, Oahu, Molokai, Lanai, Kahoolawe, Maui, and Hawaii. The smaller leeward islands from Nihoa and Necker and beyond to Midway and Kure were studied by the Tanager Expedition, and the list of vascular plant collec-

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³ The matter has recently been re-investigated by Dr. R. Wilbur (Pacif. Sci. 18(1):101-103, 1964), who concludes that "*G. sandwicense* Parl." is the correct name for the Hawaiian native cotton, not "*G. tomentosum* Nutt." as used throughout this article.

tions (Christopherson and Caum, 1931:20-39) includes only one malvaceous species, *Sida fallax*. Nor was *tomentosum* found on the small island of Molokini, which lies in the channel between Kahoolawe and Maui, by Forbes (1913a:10).

Collections from five of the eight major islands are preserved in the herbarium of the Bernice P. Bishop Museum. A total of 40 accessions includes no specimens from the other three islands, Niihau, Kauai, and Hawaii. Niihau is a privately owned cattle ranch, and few botanists have had the opportunity to visit it. Mrs. Sinclair (1885:23) included a painting of *tomentosum* in her "Indigenous Flowers of the Hawaiian Islands" which, according to St. John (1954:144-145), was probably made from living material near her home in Keikei, Niihau. The only published record of *tomentosum* on Niihau is that of Forbes (1913b:23).

I have been able to find only one definite record of the occurrence of this species on Kauai. This is a very old record (Wawra, 1873) which was kindly drawn to my attention by Dr. O. Degener. In recent years it has apparently not been seen, though St. John (loc. cit.) listed it among plants common to Niihau and Kauai. Ripperton and Hosaka (1942) did not record it from Kauai, and Mr. Stephen Au and Mr. A. W. Duvel, who are familiar with the botany of the island, inform me that they have never seen it there. Dr. C. M. Rick recently searched for it among the dry western foothills in the Mana-Kekaha region without success. This suggests that *tomentosum* is very rare, or possibly extinct, on Kauai.

Concerning Hawaii, there is a rather puzzling conflict of evidence. MacCaughy (1917:414-418) described *tomentosum* as one of the species adapted to the colonization of lava flows, with an altitudinal range of 0-2000 ft. Although he did not state explicitly that the species occurred on Hawaii, his paper was concerned entirely with the (geologically) recent flows which are confined to Hawaii and East Maui. I have been able to find no independent record of the occurrence of *tomentosum* in either of these areas. Further, an altitude of 2000 ft is a considerably higher elevation than any recorded for the Bishop Museum collections, or found during the present study. As will be evident later, *tomentosum* is usually found as a component of *Prosopis*

scrub, the altitudinal ranges of which have been mapped for the Hawaiian Islands by Ripperton and Hosaka (1942:maps 1-3). According to their maps there is one—and only one—region where this type of vegetation ("Zone A" in their terminology) extends to an elevation of 2000 ft. This is the Kau Desert region in south-east Hawaii, and if MacCaughy's statements concerning *tomentosum* applied to Hawaii, this would seem to be the only region which could have provided the necessary range in altitude. On the other hand, botanists who are very familiar with the Hawaiian flora (Miss Marie C. Neal, Mr. L. W. Bryan, and Mrs. C. K. Wentworth) have informed me that they have never seen the species on Hawaii, except in culture. It was not listed by Ripperton and Hosaka (1942) as a component of their "Zone A" vegetation on Hawaii, nor by Fagerlund and Mitchell (1944) in their check list of plants in the Hawaii National Park.

The map in Figure 1 shows the probable geographic range of *tomentosum* as it exists today. Sites collected during the present study are indicated by solid circles. These do not differ materially from earlier collections recorded in the herbarium of the Bishop Museum. Sites recorded by earlier collectors, but not checked during the present study, are represented by solid circles enclosed in rings. The open circle shows the locations of hybrid populations on Oahu which will be considered later. Shaded portions of the map show the approximate areas in which the average annual rainfall is 20 inches or less (Leopold, 1951:2).

In the case of the Oahu populations the apparent negative relation between rainfall and collection sites is quite significant, since the time available allowed for a careful search to be made on an island-wide basis, and no populations were found outside these dry areas. Elsewhere, owing to time limitations, only the drier areas were carefully studied. However, none of the collections in the Bishop Museum for which locations are recorded, appears to have been collected outside the low rainfall areas, and it seems likely that in the neighbor islands, as in Oahu, rainfall is a primary factor limiting the range of the species.

The negative relationship between rainfall and habitat is also indicated by the altitudinal

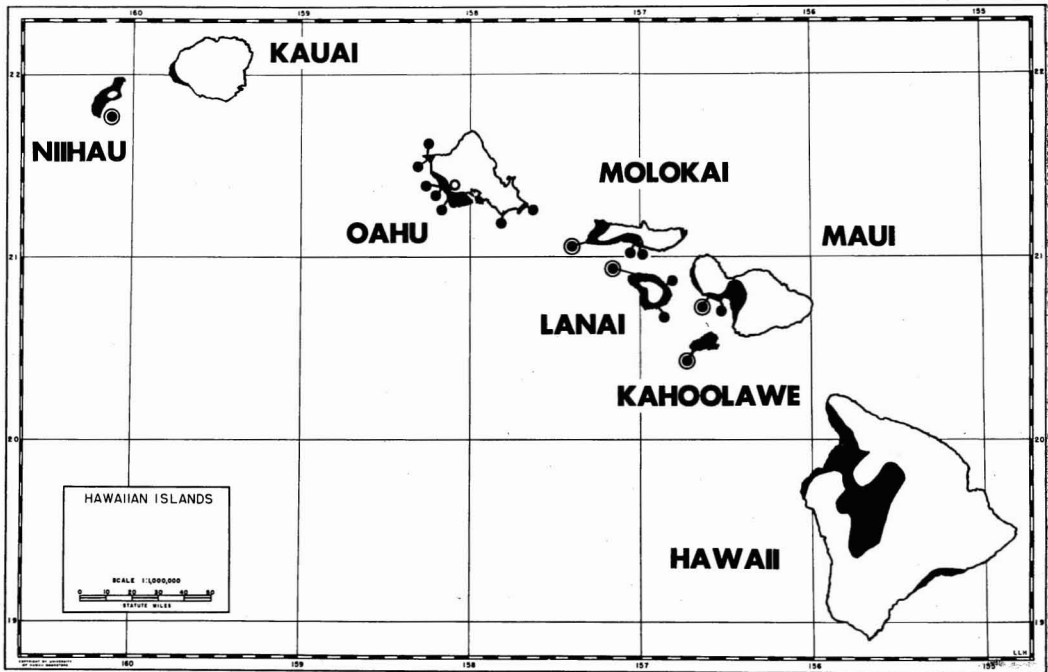


FIG. 1. Geographic range of *Gossypium tomentosum* Nutt. in the Hawaiian Islands (1963). Solid circles indicate collection sites; those enclosed in rings represent sites of former collections unchecked during the present study. The open circle indicates site of hybrid populations. Shaded areas correspond to regions with an average annual rainfall of 20 inches or less.

range of the species. On Oahu rainfall rises rapidly with elevation, and *tomentosum* was not found above an altitude of 100 ft. On Lanai, a low island in the rain-shadows of Molokai and Maui, scattered populations were found extending from sea level to almost 1000 ft. The collections from Molokai and Maui were obtained between 100 and 250 ft. These differences in altitudinal ranges agree quite well with the vegetation maps published by Ripperton and Hosaka (loc. cit.).

ISLAND HABITATS

1. Oahu

As shown in Figure 1, *tomentosum* is found most extensively on the western coastal plain in the rain-shadow of the Waianae Range. Here it extends in scattered populations from the southern extremity of the range, north of Barber's Point, to the outskirts of Nanakuli. North of this village is another population around Maile Point and extending for about 2 miles

inland along the Hakimo Valley. Elsewhere along the coast only scattered plants were found around Kaena Point (from north of Makua extending around the point to the north coast). South of Nanakuli, *tomentosum* is found almost exclusively as an understory, along with *Sida* spp. and occasional *Opuntia*, in *Prosopis* (keawe)* scrub. It appears to grow best under partial shade, i.e., wherever the stands of *Prosopis* are relatively thin. A similar habitat occurs around Maile Point, but there a semiproculumbent form (ecotype or plastic variant?) has extended away from the scrub to the edge of the exposed beach. Inland it extends along the Hakimo Valley as a component of mixed *Prosopis* and *Leucaena* scrub. On the whole the populations are found most commonly on the coastal flats, extending a little way up the slopes of the Waianae Range, but not ascending to a height of more than 100 ft. On the ocean side they rarely extend to the strand; the Maile Point population is exceptional in this respect.



A relic population occurs at the southern limit of the Koolau Range, west of Makapuu Point. Earlier records suggest that this population may once have extended farther west, at least to Koko Head and possibly as far as Diamond Head. All the area west of Koko Head is being absorbed rapidly in housing developments. The relic population is found along the roadside and extending inland to the west of the Mauka Kai golf course. Here the former cover of *Prosopis* has been cleared in recent years and the present habitat is obviously not a natural one. A small population is also found as a component of *Prosopis* scrub inside Diamond Head Crater.

Two other interesting features of the habitat are worth noting at this time, since they apply to the other islands also. Without exception the wild cotton was not found growing in friable soil, but always rooted deeply among outcrops of volcanic boulders, presumably the results of ancient lava flows. It was always found in association with *Sida*, but was far more restricted than the latter in range and habitat. Three different habitats on Oahu are illustrated in Figure 2.

2. Molokai

According to Degener (1937:fam.221), *tomentosum* is commonly found in the dry southwest end of the island, but is rare elsewhere except in the Kawela area, east of Kaunakakai. Unusually heavy rains prevented a visit to the main region, which is only accessible by traces crossing the pineapple plantations west of Maunaloa. The most recent collection from this area appears to be Degener no. 9589 (Bishop Museum) which was collected at Kamakaipo in 1928.

Two populations, both of limited size, were found along the coastal region between Kaunakakai and Kawela. One of these occurred on a moderate slope about 50 ft above the highway, 2 miles east of Kaunakakai under a thin stand

of *Prosopis*. It was absent among the taller stands bordering the highway and did not extend to an elevation of more than 100 ft inland. The other population consisted of thinly scattered plants rooted among large volcanic boulders lining the sides of Onini Gulch in the Kamiloloa-Alii Pond district. The population extended from approximately 150–250 ft elevation. At lower levels, plants were not found among the dense stands of *Prosopis*, nor at higher levels where *Prosopis* was replaced by *Leucaena*. No other populations were found in a search extending as far east as Kamalo.

3. Lanai

The range of *tomentosum* appears to be greater on Lanai than on any of the other islands. At sea level on the south coast around Manele Bay and near the east coast in the Keomuku district there are areas where it forms an almost solid understory in tall *Prosopis* scrub. At higher elevations the populations thin out, and in the neighborhood of 1000 ft scattered plants occur in quite exposed positions, rooted on old lava flows among low and sparse vegetation. In such open habitats *tomentosum* occurs as a sprawling or semiprocumbent shrub and the characteristic tomentose surface of stems and leaves becomes intensified. Time did not permit collection on the north coast of the island, which is not readily accessible. A collection from this area (Awalua) was made in 1961 by Kondo (nos. 1b and 1c in the Bishop Museum). It seems likely that it is a common plant all around the periphery of the island in those areas which have not been brought in to pineapple cultivation.

4. Maui

No collections have been recorded from the eastern, and geologically much younger, region of this saddle-shaped island. The herbarium in the Bishop Museum has two collections, both made by Degener (nos. 3650, 17624), in or near Pohakea Gulch, which is situated above

FIG. 2. Typical habitats of *G. tomentosum* on Oahu. Photographs by C. M. Rick.

- (a) Under *Prosopis* cover, near Barber's Point
- (b) Volcanic boulders in dry gulch, near Kahe Point
- (c) Exposed beach, near Maile Point

the eastern coastal plain on West Maui. In 1962 another population, 10 miles west of this area, near Ukumhame Shaft, was collected by Mr. Craig Whitesell. According to his notes, the population was scattered over 2-3 acres at about 250 ft elevation. This population was not located during the present study, but plants were found in the Pohakea Gulch region at an elevation of about 100 ft. These occurred under a thin cover of *Prosopis* immediately above a cane field and extending up into the gulch.

Most of the dry area in the "saddle" of the island which is shown in Figure 1 is in cane cultivation. Judging by the habitat of *tomentosum* on the other islands, the only likely area for its occurrence on East Maui would be the dry southernmost region lying between Makena and Kamanamana Point. Its vegetation is composed principally of tall *Prosopis* scrub with frequent *Opuntia*, which is traversed in places by bare, or almost bare, lava flows. This area was visited but no *tomentosum* was found.

5. Kahoolawe

This island is uninhabited and has been used for some years by the U.S. Navy as a target for bombing practice. Its low-altitude location in the rain-shadow of Maui and a past history of heavy overgrazing combine to make it the most barren of all the major islands in the group. From the air it appears as a low plateau, practically devoid of vegetation, with dry scrub lining the steep gullies which surround its coast. Fifty years ago Forbes (1913a:7), on the last recorded botanical exploration of the island, found a population of *tomentosum* near the southwest end.

6. Hawaii

Three areas which would seem to offer appropriate habitats for the establishment of the species were searched without success:

- (a) The dry coastal flats north of Kona Airport, Kailua
- (b) The area bordering the coastal road between Kealahou Bay and the City of Refuge in the South Kona District
- (c) A small area between Honuapo and Punaluu Beach in the southern Kau District

Time did not permit a visit to the Kau Desert and Hilina Pali areas which, as noted earlier, may have provided the necessary combination of altitudinal range and vegetational type for MacCaughy's observations.

CLIMATE AND "SOIL"

The climatic conditions to which *tomentosum* is adapted would appear to differ rather sharply from those under which the wild forms of *hirsutum* flourish in the Caribbean. Honolulu weather records from 1948-1960 indicate that the average temperature on coastal Oahu varies (in round figures) between 70 and 80 F, with a mean of about 75 F, and a diurnal range of 9 F. The winter (short-day) months tend to be cool and wet, though the monthly distribution of rainfall is very erratic. In contrast, the Caribbean climate has a higher mean temperature, and short day length usually coincides with a pronounced dry season and cooler night temperatures. The Caribbean cottons grow vegetatively during the long wet days, and flower and set seed during the dry season. Flower initiation seems to be determined in part by day length and in part by night temperature (Mauney and Phillips, 1963), so that there is a seasonal flowering cycle. This regular cycle is missing in *tomentosum*. Mrs. Sinclair (1885:23) noted that it flowered the year round; and the herbarium specimens in the Bishop Museum were collected in every month of the year except December. During the present study it was found that in any population—at least from February through May—most of the plants are vegetative and the remainder may have young flower buds, open flowers, or ripe bolls. Seeds can therefore be collected over a long period, but only from relatively few plants at any given time.

Although *tomentosum* can be considered a dry-land plant, it appears to be less xerophytic than Caribbean *hirsutum*. Wild forms of the latter species will often thrive around salt ponds, and immediately exposed to strong winds and salt spray. Forms which grow in dry scrubland away from the coast tend to be components of more open vegetation, or else to grow tall. Typically they are not found as an understory among taller plants. In contrast, the most vig-

orous stands of *tomentosum* were found under light shade.

The virtual restriction of *tomentosum* to old volcanic outcrops, as opposed to friable soil, suggests that it possibly may have rather specialized physical and nutritional requirements. MacCaughey (loc. cit.) included it in a list of species which he considered to be particularly adapted to the colonization of lava flows and which were characterized by certain xerophytic features. Some of these features are clearly applicable to *tomentosum* (viz., woody perennial growth form, with slow growth and deep root penetration; foliage often pubescent; and a tendency to assume a decumbent habit on bare substrates). He also pointed out the extremely xerophytic conditions which are generated on recent lava flows through a combination of high evaporation, free drainage, and rapid heating of black or almost black surfaces. However, these conditions apply particularly to recent lava flows, and in the present study no *tomentosum* was found in those areas (Hawaii and East Maui) to which recent flows are restricted.

It seems likely that some of the difficulties of growing the species in culture may be associated with (a) failure to provide sufficiently rapid drainage, (b) too high a mean temperature, and (c) too acid soil conditions. With regard to the third factor, MacCaughey (1917: 408) noted that soils derived from Hawaiian lava flows have a far higher proportion of basic constituents than comparable mainland soils (64% as compared with 19%, according to his figures). The following analysis of igneous rocks in Hawaii was obtained from "Handbook of Hawaiian Soils" (1935):

Average of 56 Analyses of Lavas from
Island of Hawaii

SiO ₂	50	Na ₂ O ₃	3
Al ₂ O ₃	14	K ₂ O	1
Fe ₂ O ₃	3	Ti ₂ O ₂	3
FeO	9	P ₂ O ₅	0.5
MgO	8	MnO	0.1
CaO	9		

MORPHOLOGICAL VARIATION

Those morphological characteristics of *tomentosum* which distinguish it taxonomically

from the other New World species of *Gossypium* (long anther filaments, partly fused in pairs; absence of leaf nectary; intense yellow flower color; undifferentiated and strongly adherent seed fibers) were found to be quite uniform. On the other hand, characters which previous experience had shown to be rather variable (leaf shape; bracteole form and dissection; degree of pubescence; plant habit) were found to be extremely variable. There was little if any tendency for these variations to follow a geographical pattern; i.e., it was not possible to distinguish morphologically between different island races. In this respect, *G. tomentosum* contrasts strongly with the native species of the Galapagos Islands (*G. darwinii*), in which each island has tended to develop its own well-marked morphological race. It is somewhat surprising that two archipelagos, of comparable size and origin, and offering similar arid habitats to related colonizing species, should have produced such different evolutionary results.

The nature of variation in leaf shape and bracteole form is illustrated in Table 1 and Figure 3, respectively. The data show the considerable range of variation within any one population, and the extensive overlap that exists when different populations are compared. Varia-

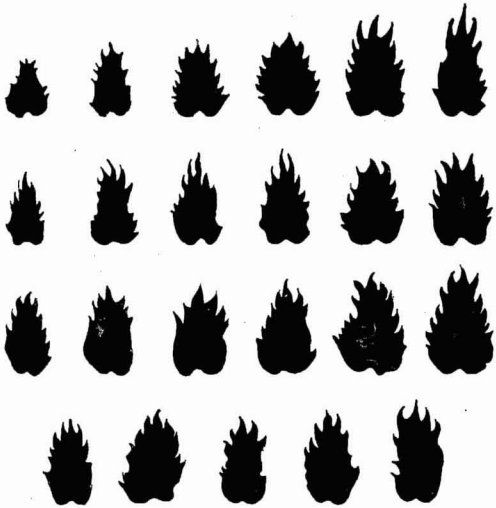


FIG. 3. Outline drawings, approximate half natural size, of *tomentosum* bracteoles. All bracteoles were obtained from open flowers. Top row, Oahu; 2nd row, Lanai; 3rd row, Molokai; 4th row, Maui.

TABLE 1

VARIATION IN LEAF SHAPE IN 11 POPULATIONS OF *Gossypium tomentosum*
COLLECTED FROM FOUR DIFFERENT ISLANDS*

(Measurements based on ten mature leaves per population)

L—Length of leaf in mm from pulvinus to tip of median lobe

S—Length of sinus in mm from pulvinus to base of median lobe

Index—*S* expressed as a percentage of *L*

		<i>L</i>	<i>S</i>	<i>Index</i>	
				<i>Mean</i>	<i>Range</i>
OAHU	1. Barber's Point—Kahe Point.....	84.1	32.2	38.3	31-49
	2. Kahe Point—Nanakuli.....	78.8	30.8	39.1	28-49
	3. Maile Point (procumbent form).....	80.0	29.0	36.3	30-45
	4. Maile Point (shade form).....	100.0	39.4	39.4	31-46
	5. Makapuu Point.....	79.6	32.4	40.7	36-47
MOLOKAI	6. Kaunakakai.....	74.7	28.8	38.6	27-50
	7. Onini Gulch (100 ft elev.).....	64.4	24.7	38.4	35-45
	8. Onini Gulch (200 ft elev.).....	81.0	34.6	42.7	36-49
LANAI	9. Keomuku.....	71.1	32.4	45.6	38-53
	10. Manele.....	71.7	31.2	43.5	36-55
MAUI	11. Pohakea Gulch.....	71.1	33.0	46.4	42-51

tions in both characters appear to be essentially random. On the other hand, variations in pubescence and plant habit were markedly correlated with local environmental conditions to which the plants happened to be exposed. Plants growing in exposed situations usually had a sprawling or semiproscumbent habit, and the leaves were covered with a dense tomentum giving them a bluish-grey appearance. Under *Prosopis* cover individual plants were found which grew as high as 9 ft, and the leaves were finely tomentose with a dusty green color.

Experimental studies have shown that in New World cottons, pubescence and plant habit can be influenced strongly by environmental conditions, particularly light intensity; both characters are also sensitive to changes in genotypic background. For instance, a single major gene determines the finely tomentose surface of *tomentosum*. When the gene is transferred by backcrossing to a *hirsutum* background, the leaf surface becomes densely hairy and phenotypically indistinguishable from the *hirsutum* mutant form "Pilose." The degree of hairiness can also be modified to a lesser extent by transferring the plants from a shaded greenhouse to full sunlight. Comparative studies under controlled environmental conditions would therefore be necessary to determine whether the variation observed in

natural stands of *tomentosum* is phenotypic only or the result of ecotypic differentiation.

POLLINATION AND INTROGRESSION

1. The Primary Breeding System

It has been pointed out by Baker (1955:347-349) and Stebbins (1957:343-344) that an autogamous breeding system would be initially advantageous to a colonizing plant species, since it would render the latter independent of pollen vectors. On the contrary, it would be most unlikely for appropriate pollen vectors to be introduced into a new habitat along with the cross-pollinated species dependent upon them. This argument is particularly pertinent if applied to the colonization of isolated volcanic islands like the Hawaiian group.

All species of *Gossypium* are self-compatible with radially symmetrical flowers, large numbers of anthers, and a true floral nectary located in a deep circular groove lined with glandular hairs at the inner base of the calyx. The nectary can be seen only under low-power magnification of a vertical section of the receptacle. It is accessible both to long-tongued insects and to insects small enough to crawl between the bases of the petals. Usually there are also extrafloral nectaries located (1) at the bases of the bracteoles and (2)

on the outer surface of the calyx alternating with the bracteoles, and there is a leaf nectary on the midrib of the under surface of each leaf. It is thus possible for insects to obtain nectar without entering the flowers at all. These characteristics do not suggest floral adaptation to any specific insect vector (Grant, 1950:392).

In *tomentosum* extrafloral nectaries and leaf nectaries are lacking entirely, but a true floral nectary can be seen in vertical section. There is reason to suppose that the latter is nonfunctional or only weakly functional. When the corolla is removed from a fresh flower of *barbadense* or *hirsutum*, a pool of nectar can be seen within the calyx cup, but the secretion is weak or absent in *tomentosum*. This observation, based on the relatively few flowers available at the time of study, was confirmed later by Mr. Frank Johnson. He informs me that only a fraction of the flowers he examined appeared to contain nectar. It seems likely, therefore, that insects would visit *tomentosum* flowers primarily to feed on pollen or to gather pollen. Further, because a limited number of plants are in flower at any one time in *tomentosum* populations, they would not be likely to furnish a main source of supply to pollen-gathering insects. Under these circumstances a mainly autogamous breeding system is to be expected, with visits by pollen-gathering insects restricted to temporary periods of over-all pollen shortage.

In Central America and the Caribbean, the relatively small and scattered populations of wild and dooryard forms of *G. hirsutum* do not impress the observer as being heavily stocked with pollinating insects. Those commonly found in the flowers are small ants and beetles which probably function more effectively as agents of self- rather than cross-pollination. The situation in *tomentosum* populations appears to be similar, though the number of observations which could be made was too small to be very reliable. Unusually heavy and persistent rains occurred throughout March and well into April in this normally dry habitat; thereafter there was a temporary cessation of flowering until toward the end of May. In the latter part of April the combined results of three separate searches through the Oahu populations yielded less than 50 flowers. It was noted that although honeybees and small moths (occasionally) and carpenter

bees and scavenger flies (rarely) were visiting *Sida* flowers in the immediate neighborhood, none of these potential pollinating agents visited *tomentosum* flowers. Most of the latter were entirely devoid of insects, though occasional flowers containing a few small ants or fruit-bud beetles (*Conotelus mexicanus*) were seen.

These observations, though limited, do not suggest that insects play an important role in the breeding system of *tomentosum*. On the other hand, a strictly autogamous system is difficult to reconcile with the fact that *tomentosum* flowers, like those of other wild forms of the New World species, have long styles with the receptive stigmatic surfaces borne high above the staminal column (cultivated forms usually have short styles with the stigmatic surfaces in contact with, or immediately above, the staminal column). An interesting feature of the *tomentosum* style is the fact that it is often recurved, assuming a crozier-like structure with the stigmatic surface nearly approximated to the staminal column.

2. The Effects of Insect Introduction

In oceanic islands like the Hawaiian group with a numerically poor indigenous insect fauna (Zimmerman, 1948:94-95), the introduction of beekeeping as a local industry could have potentially disturbing effects on the taxonomy of the local flora. A likely example is provided by the dooryard cottons (*G. barbadense*), which still may be found in gardens and along roadsides on the islands. As early as 1812, cotton was introduced into Oahu (Jones, 1937:17) and, later, in the early 20th century, serious attempts were made to establish it as a crop (Krauss, 1909:1-16). Commercial varieties of Sea Island (*barbadense*) and Upland (*hirsutum*) were both introduced without lasting success. Around 1857 the first shipment of honeybees arrived from California (Eckert, 1951:1). According to Van Dine and Thompson (1908:8), *Prosopis* soon became the primary source of nectar, and on the western side of the island apiaries were moved to the coastal areas under the shelter of the *Prosopis* forests, where many of them are found today. During the past 10 years this source of nectar has been seriously diminished by the activities of an immigrant moth, *Ithome concolorella*, which destroys the

florets of *Prosopis* and certain other leguminous shrubs (Namba, 1956:100). As a consequence the relatively flower-constant honeybee has been forced to forage among a variety of nectar (and pollen) sources.

The village of Nanakuli is located on a crescent-shaped coastal plain of western Oahu, bounded by the Waianae Range which juts into the sea to the north at Maile Point and to the south at Kahe Point. The lower slopes of the range are dominated by a zone of *Prosopis* scrub, and where this zone approaches the coast, populations of *tomentosum* are very common in the understory. Occasional *barbadense* plants occur along the coastal highway which runs through Nanakuli, and also in gardens in the village itself. In two small areas, (a) south of Piliokahe Beach and (b) in a waste lot adjoining the Texaco Service Station in the village, outlying plants of *tomentosum* and *barbadense* are growing within 50 yards of each other. Less than a quarter mile inland, two colonies of honeybees are established in hives under the *Prosopis* trees. And in the areas where *tomentosum* and *barbadense* are in close proximity, two obviously hybrid populations are found whose taxonomic properties are illustrated by the data presented in Table 2 and Figure 4.

Table 2 gives the results of scoring the popu-

lations for four qualitative or semiquantitative characters which distinguish the two species. The scoring was necessarily limited to those plants which were flowering at the time the study was made. The 11 plants scored include 9 different combinations of characters, none of which was identical with either parental combination. The populations were therefore segregating for characters which distinguish the two species.

The plants were also scored for certain metrical characters which previous experience has shown to be useful in discriminating between species of New World cottons. These are presented as a scatter diagram in Figure 4, according to the methods developed by Anderson (1949: 81-101). The characters measured are listed below; methods of measurement will be found in the Appendix to this paper:

- Br. T.—Number of bract teeth
- Br. D.—Bract dissection index
- Br. S.—Bract size
- L. I.—Leaf index
- P. L.—Petal length
- S. I.—Staminal index

In Figure 4 staminal index is plotted on the horizontal axis, petal length on the vertical axis. The other characters are symbolized according

TABLE 2

HYBRID COTTON POPULATIONS AT NANAKULI, OAHU; SEGREGATION IN QUALITATIVE CHARACTERS

Symbols used: *H* (*tomentum*); *Ne* (leaf nectary); *Y* (bright yellow petal); *R* (petal spot). Presence of each character is indicated by (+), absence by (○) and intermediate condition by (—).

	<i>H</i>	<i>Ne</i>	<i>Y</i>	<i>R</i>	
<i>tomentosum</i>	+	○	+	○	Parent type; in <i>Prosopis</i> scrub south of Nanakuli
	+	○	+	○	
Hybrid No. 1.....	—	—	+	—	Waste ground near service station, Nanakuli
2.....	+	—	○	○	
3.....	○	—	+	—	
4.....	○	+	+	+	
5.....	—	—	+	—	
6.....	—	—	—	—	Roadside behind Piliokahe Beach, Nanakuli
7.....	—	○	+	—	
8.....	○	—	—	+	
9.....	—	○	+	—	
10.....	+	—	+	+	
11.....	—	○	+	+	
<i>barbadense</i>	○	+	—	+	Parent type; Dooryards, Nanakuli
	○	+	—	○	

to the key accompanying the figure. Solid circles refer to the parental species (*barbadense* to the left, and *tomentosum* to the right of the chart). Open circles represent the plants under study, the "Texaco" plants being distinguished from the "Piliokahe" plants by dots placed within the circles.

It is evident that although most of the plants resemble *barbadense* with respect to the characters measured, they all deviate in one or more characters in the direction of *tomentosum*. This would be expected if they were hybrids segregating from backcrosses of *tomentosum* to *barbadense*. A few of the plants had open bolls, and the seeds they contained bore fibers of two distinct kinds—medium to long lint fibers, more or less adherent to the seed-coat; and coarse, strongly adherent fuzz fibers. Both lint and fuzz fibers were light brown in color. These fiber characteristics are typical of *barbadense* \times *tomentosum* hybrids studied previously in culture.

Several visits were made to the hybrid populations from the beginning of March through May, but at no time was insect activity among them very great. The pollen-feeding beetle (*Conotelus*) was quite common inside the open flowers, but it is not likely that it would be effective as a cross-pollinating agent. A few small ants were also found in the flowers from time to time, but the only "prospects" likely to be concerned in natural crossing were the rare visits by honeybees, and one solitary visit by a syrphid fly, which were observed. Similarly, it was noted that *Conotelus* was common inside the flowers of dooryard *barbadense* in the same area, and rather infrequently honeybees were seen to enter the flowers also. A few carpenter bees and hornets were observed around the plants, but their attention appeared to be confined to the extrafloral nectaries, and they were not seen to enter the flowers. During the same period honeybees in particular, syrphids, and occasionally carpenter bees and small moths were seen to be actively visiting the flowers of *Sida* and a variety of garden ornamentals in the neighborhood.

Thus it appears that rather infrequent visits by honeybees were most likely responsible for the origin of the hybrid populations, and for the subsequent backcrossing and intercrossing which have probably taken place. However, the

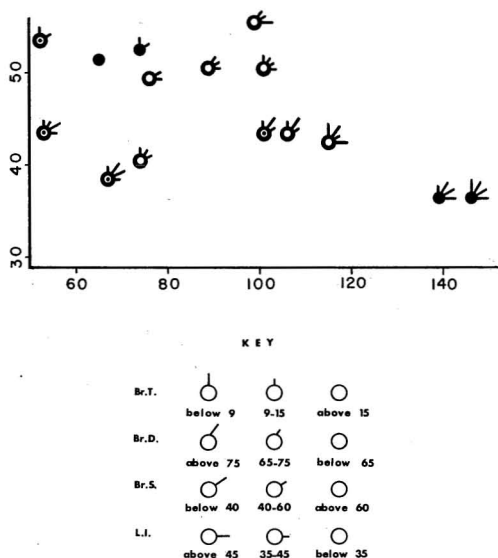


FIG. 4. Scatter diagram showing variation pattern in hybrid populations at Nanakuli, Oahu. Staminal index plotted on horizontal scale, petal length on vertical scale. Other characters indicated according to key. Further explanation in text.

relatively few observations which could be made on *tomentosum* provided no direct evidence that honeybees, or any other pollen-gathering insects, visit flowers of this species.

LOCAL NAMES AND USE

There are two Hawaiian names for *Gossypium tomentosum*: *ma'o* ("yellow-green") and *bulu bulu* ("hairy hairy"). Two independent sources suggest that the plant was used by the ancient Hawaiians as a source of green dye for their kapa cloth. Malo (1903:43, 74), writing about 1836, stated definitely that *ma'o* was *Gossypium tomentosum*, and that its flower was used as a dye to color "tapa and the loin cloths of the women etc." Bennett (1840:217), who was a surgeon on a whaling ship, stated that "a delicate green-yellow dye" obtained "from an infusion of the flowers of the cotton plant" was used for dyeing kapa in Oahu. Later in the same narrative (1840:255) he said: "Several exotic kinds of the cotton-shrub (*pulu* or soft of the natives) grow wild in the plains, and include that rare species, the yellow or nankeen cotton (*Gossypium religiosum*) called by the natives *marou*."

Brigham (1911:50, 144) referred to Bennett's statement, and assumed that the latter had con-

fused cotton with *Abutilon incanum*, which also had the Hawaiian name *ma'o* and which also was used as a dye. That Brigham was in error is suggested from the following considerations:

- (1) Bennett's use of the (then) accepted Latin nomenclature in identifying the numerous plants he described in his narrative, indicates that he was a competent botanist.
- (2) Bennett stated explicitly that the flowers were used as a source of the dye: according to Brigham it was the leaves of *Abutilon* which were used.
- (3) The name *ma'o* is applied both to *G. tomentosum* and to *A. incanum*. The name is incomprehensible as a description of either plant, but quite understandable if it refers to a common dyeing property.
- (4) The word "nankeen" was used non-specifically in the 18th and 19th centuries to describe a brown-fibered cotton. It was applied both to Asiatic and to New World cottons and could reasonably have been applied by Bennett to the brown-fibered *tomentosum*. Bennett's identification of this species as "*G. religiosum*" is consistent with other nomenclature of the same period. (An obvious specimen of *G. tomentosum*, no. 12935 in the National Herbarium, Washington, D.C., which was collected in 1845 by the U.S. Exploring Expedition under the command of Charles Wilkes, is labelled "*Gossypium religiosum*.")
- (5) It has been known for some time that the flowers of the cotton plant contain pigments, once thought to be of potential importance to the dyeing industry (Perkin, 1899:825). Dr. C. R. Parks (1963) has recently made a chromatographic survey of these pigments and has shown that the depth of the yellow color in the petal is primarily determined by the relative amount of the flavonol pigment, gossypetin, which it contains in various glycosidal forms. Further he has shown that the petals of *tomentosum* have larger amounts of this pigment than those of other species. (This explains the bright

sulphur-yellow shade of *tomentosum* flowers, as compared with the lemon-yellow of *barbadense* and the cream shades of many *hirsutum* forms). Solutions of gossypetin glycosides are bright yellow in color, but separate out in greenish crystals when concentrated. Slightly alkaline solutions produce a green dye. According to Bennett (loc. cit.), the "astringent water of the taro patch" was used to mordant the dye—possibly a matter of pH adjustment.

The other Hawaiian name, *bulu bulu* ("hairy hairy"), does not seem to be a particularly apt description of the finely tomentose surface of the plant. One wonders whether the name may not, in fact, be a corrupted version of *booluu*, which, according to Brigham (1911:171) is "the principal Hawaiian word meaning to color . . . to dive into the water, to plunge into a liquid, hence to dye. . . ."

SUMMARY

1. The wild cotton of the Hawaiian Islands, *G. tomentosum* Nutt., has never been found beyond the limits of the eight major islands of the group. Today it is only known on six of the islands: Niihau, Oahu, Molokai, Maui, Lanai, and Kahoolawe. There is apparently no definite record of its occurrence, or former occurrence, on Hawaii, despite general statements to that effect in the literature.

2. Within its current geographical range, the species is found only in dry areas with an average annual rainfall of 20 inches or less. Its altitudinal range on any particular island therefore depends on local topography and position relative to rain-shadows.

3. The most common habitat is as an understory in thin *Prosopis* scrub, growing among partially weathered volcanic boulders. Less frequently it is found in more exposed positions, i.e., near beaches or (at relatively high altitudes) among thin low scrub.

4. The species has not evolved morphologically distinct island races. Those morphological characters which differentiate it taxonomically from other species of *Gossypium* are remarkably uniform. Other characters may vary apparently

at random (leaf shape and bract form), or may be associated with the particular environment in which the plant is growing (pubescence and plant habit).

5. In one area in Oahu two populations were found of undoubtedly hybrid origin (*G. barbadense* × *G. tomentosum*). The underlying reasons for this situation are discussed.

6. Evidence is presented for the belief that the flowers of *G. tomentosum* were used by the ancient Hawaiian people as a source of green dye.

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APPENDIX

Methods of measuring characters shown in Figure 4:

- Br. T.*—The average number of teeth per bracteole, based on counts of 10 bracteoles.
- Br. D.*—Bract dissection index: S expressed as a percentage of L , where S is the distance from bracteole base to base of the sinuses on either side of the median tooth, and L is the distance from bracteole base to apex of median tooth. Measurements averaged from three bracteoles each removed from a flower in bloom.
- Br. S.*—Bract size: The geometric mean of bracteole length and bracteole breadth. Averaged from three bracteoles, each removed from a flower in bloom.
- L. I.*—Leaf index: S expressed as a percentage of L , where S is the distance from leaf pulvinus to base of median lobe, and L is the distance from leaf pulvinus to apex of median lobe. Measurements averaged from three climax leaves.
- P. L.*—Petal length, measured from claw of petal to maximum distance on outer edge. Averaged from three fresh petals from different flowers.
- S. I.*—Staminal index: Maximum diameter of staminal column expressed as a percentage of the length of the column. Measurements averaged from three flowers.